

THE TAXONOMIC RESURRECTION OF *QUERCUS* *LACEYI* SMALL (FAGACEAE)

KEVIN C. NIXON

L.H. Bailey Hortorium
Cornell University
Ithaca, NY 14853, U.S.A.

CORNELIUS H. MULLER

Department of Biological Sciences
University of California
Santa Barbara, CA 93106, U.S.A.

ABSTRACT

Quercus laceyi Small, a white oak (*Quercus* sect. *Quercus*) described in 1901 from limestone hills on the southern part of the Edwards Plateau of Texas, has been treated as a synonym of *Quercus glaucoides* Mart. & Gal. in recent literature. However, *Q. laceyi* is clearly a species distinct from *Q. glaucoides*, based on vegetative, floral, fruit, and embryological characters. In addition to the Edwards Plateau, *Q. laceyi* is found on limestone mountains of Nuevo Leon and Coahuila, Mexico, but does not overlap in distribution with *Q. glaucoides* sensu stricto. The latter species has a natural distribution in central and southern Mexico, from San Luis Potosi south to Oaxaca. *Quercus glaucoides* is the type species of subsection *Glaucoideae*, a group of about 30 – 35 species in the southwestern United States, Mexico, and Central America, which share the synapomorphy of fused cotyledons. *Quercus laceyi*, on the other hand, has free cotyledons, and is probably more closely related to the lobed-leaf white oaks (e.g., *Quercus alba* L.) of the eastern United States. A key and descriptions are provided for the two species.

RESUMEN

Quercus laceyi Small, un encino blanco (*Quercus* sect. *Quercus*) descrito en 1901 de colinas calizas en la parte sur de la Planicie Edwards en Texas, ha sido tratado como sinónimo de *Quercus glaucoides* Mart. & Gal. en la literatura reciente. Sin embargo, con base en caracteres vegetativos, florales, fructíferos y embriológicos, es obvio que se trata de dos especies distintas. *Quercus laceyi* se encuentra tanto en la Planicie Edwards como en las montañas calcáreas de Nuevo Leon y Coahuila, México, y su distribución no coincide con la de *Q. glaucoides*. Esta última especie tiene una distribución natural en el centro y sur de México, desde San Luis Potosí hacia el sur hasta Oaxaca. *Quercus glaucoides* es la especie tipo de subsección *Glaucoideae*, un grupo de alrededor de 30 – 35 especies en el suroeste de los Estados Unidos, México y América Central, que presentan cotiledones fusionados como sinapomorfismo. *Quercus laceyi*, por otra parte, tiene cotiledones libres, y probablemente está más relacionada con los encinos blancos de hoja lobulada (e.g., *Q. alba* L.) del este de los Estados Unidos. Se provee una clave y descripciones para las dos especies.

INTRODUCTION

Quercus laceyi Small was based on material from the southern part of the Edwards Plateau of Texas (Small 1901). The species is noteworthy because of the

striking bluish-green color of the foliage that is similar in color to several other oaks of Mexico and the southwestern United States. Oddly, Trelease (1924), who was otherwise noted for a rather narrow species concept, demoted *Q. laceyi* to *Q. breviloba* Sarg. forma *laceyi* (Small) Trelease. However, *Q. breviloba* is a very different species, now considered by most workers to be a synonym of *Q. sinuata* Walt. var. *breviloba* (Sarg.) Muller (Muller 1970; Dorr & Nixon 1985) and clearly is not closely related to Small's *Q. laceyi*. Muller (1951) accepted the name *Q. laceyi* for the Edwards Plateau material as well as for material from the states of Coahuila and Nuevo Leon in adjacent Mexico. Later, Muller (1970) decided that *Q. laceyi* was a synonym of *Q. glaucoides* Mart. & Gal., a species with bluish-green leaves that is widespread in southern and central Mexico. Recent papers dealing with this species in Texas have continued to use the name *Q. glaucoides*.

Our recent studies of *Q. glaucoides* sensu lato throughout its range in Texas and Mexico have provided several characters that can be used to distinguish the northern populations (*Q. laceyi*) from the southern populations (*Q. glaucoides* sensu stricto). Trees of *Q. glaucoides* from southern and central Mexico have coriaceous, persistent leaves, typically entire, toothed or sometimes shallowly lobed, and fruit that is born on peduncles from 1 – 8 cm in length. In contrast, *Q. laceyi* from Texas and the Mexican states of Nuevo Leon and Coahuila has winter-deciduous, thinner leaves that vary from entire to more deeply lobed, and fruits that are sessile or born on short peduncles. A broad investigation of embryological characters of white oaks (Nixon 1985) has shown that *Q. laceyi* has free cotyledons in the seeds, in contrast to the fused cotyledons of *Q. glaucoides*. Based on these observations, it is apparent that two species are involved in the broad concept of *Q. glaucoides*, and it is necessary to resurrect the name *Q. laceyi* for material from Texas, Coahuila, and Nuevo Leon. The descriptions of *Q. glaucoides* in recent treatments are confounded by inclusion of *Q. laceyi*, and we present here a key and revised descriptions of the two species, with complete synonymy.

A third species from Nuevo Leon and Tamaulipas, *Q. porphyrogenita* Trel. (syn. *Q. microlepis* Trel. & Mueller), shares the characters of bluish-green leaves and free cotyledons with *Q. laceyi*, and may be one of its closest relatives. *Quercus porphyrogenita* occurs at lower elevations in the eastern foothills of the Sierra Madre Oriental in Tamaulipas and Nuevo Leon, usually on limestone. It is found typically in dry oak woodland and transition to thorn scrub, often in association with *Q. polymorpha* S. & C. and *Q. canbyi* Trel. *Quercus porphyrogenita* and *Q. laceyi* barely overlap in range, in mid-elevation canyons on the eastern side of the Sierra Madre, such as below Galeana in Nuevo Leon. Occasional specimens that appear to be intermediate in leaf characters occur in these areas, but there is no indication that hybridization between these species is common or problematic. *Quercus porphyrogenita* is easily recognized by the combination of narrow, entire leaves, short petioles, strongly cordate leaf bases, and very fine cupule scales, in addition to the elevational and habitat differences of the two species.

Other than *Q. porphyrogenita*, possible relatives of *Q. laceyi* appear to be the lobed-leaf deciduous white oaks of the eastern United States. Of these species, *Q. alba*, with a western distributional limit in east Texas, has foliar features that resemble *Q. laceyi*. Both species have whitish, erect stellate trichomes on the abaxial surface of young expanding leaves. These trichomes are deciduous very early in the season, leaving a glabrous surface on mature leaves. The shape of the leaf base is typically cuneate or tapered in both species, and occasional specimens of *Q. laceyi* from mesic sites bear leaves that approach those of *Q. alba* in depth of lobing.

The probable relationship of *Q. laceyi* to eastern North American deciduous white oaks is consistent with a biogeographic pattern exhibited in several other oak species complexes, as well as numerous other woody genera. Several of the oaks found on the Edwards Plateau are considered to have their closest relatives in species with a generally more eastern distribution. The amount of difference between the Edwards Plateau populations of these taxa and their eastern counterparts varies greatly, and this is reflected in the various taxonomic ranks which they have been accorded. Some exhibit more or less continuous variation with their eastern counterparts, and are recognized as conspecific without varietal rank (e.g. *Q. marilandica* Muench., *Q. muhlenbergii* Engelm., *Q. stellata* Wang.), others conspecific with varietal rank (*Q. sinuata* Walt. var. *breviloba* (Torr.) Muller), or as species distinct from their eastern sister species (*Q. virginiana* Miller [se U.S.] and *Q. fusiformis* Small [Edwards Plateau, ne Mexico], *Q. texana* [syn. *Q. nuttallii* Palmer, see Dorr & Nixon 1985; se U.S.] and *Q. buckleyi* [*Q. texana* of authors; Edwards Plateau and Oklahoma]).

Quercus glaucoides* and subsection *Glaucoideae

While *Q. laceyi* appears to be related to eastern North American oaks, *Q. glaucoides*, on the other hand, is a member of a separate group of Mexican and Southwestern U.S. white oaks. These species consistently have marginally fused cotyledons, waxy leaf epidermis, and erect often stipitate foliar trichomes (Nixon 1985). Additionally, some species in this group, including *Q. glaucoides*, have pilose anthers, in contrast to the glabrous anthers of *Q. laceyi* and most other white oaks. The 30 – 35 species placed in this group were previously placed in 26 different series by Trelease (1924), providing little or no basis for a discussion of their relationships. Nixon (1985) erected *Quercus* subsection *Glaucoideae* (Trelease) Camus emend. Nixon for this group of species. This required expansion of Camus' narrow concept of the subsection, which was essentially the same as series *Glaucoideae* as recognized by Trelease.

Among species of subsection *Glaucoideae*, the degree of fusion of cotyledons varies, and consequently, the central lumen between the cotyledons varies in shape and size. In *Q. glaucoides*, the material observed thus far has a lumen that broadens toward the "base" of the seed/acorn (actually the distal portion relative

to the orientation of the cotyledons and epicotyl), leaving two more or less distinct marginal areas of fusion between the cotyledons. In other species, such as *Q. oblongifolia* Torr., the fused areas are much more complete, with only a narrow central lumen that is often difficult to discern in the field unless the material is sectioned fresh and allowed to dry. During drying, the tissues shrink, and the central lumen "opens" and becomes more visible. Fusion of cotyledons in *Glaucoideae* is correlated with a germination syndrome in which a cotyledonary tube is formed that pushes the hypocotyl/epicotyl axis into the soil. The epicotyl later breaks through the wall of the cotyledonary tube as cell elongation and growth occur.

The relationships of *Q. glaucoides* to other members of subsection *Glaucoideae* are not clarified by examination of Trelease's series treatment of the oaks. Trelease (1924) erected series *Glaucoideae* and included in it four species in addition to *Q. glaucoides*. All four of these (*Q. baldoquinae* Trel., *Q. mixtecana* Trel., *Q. glaucophylla* V. Seem., and *Q. harmsiana* Trel.) are considered here to be synonyms of *Q. glaucoides*. Trelease placed three additional species in the associated series *Cancellatae* (*Q. cancellata* Trel., *Q. conjungens* Trel., and *Q. sororia* Liebm.). The first two of these species are clearly synonyms of *Q. glaucoides*. A difference of opinion exists regarding *Q. sororia*, which McVaugh (1974) placed as a doubtful synonym of *Q. splendens* Nee, and which treatment we follow here. Bello-G. and Labat (1987) considered *Q. sororia* a distinct species and did not mention *Q. splendens*, but cited under *Q. sororia* a collection (*Hinton 15081*) cited previously by McVaugh as *Q. splendens*. It is clear that the concepts of *Q. splendens* of McVaugh and *Q. sororia* of Bello-G. and Labat are equivalent. This species, which we refer to *Q. splendens*, is closely related to *Q. glaucoides* and is sympatric with it in some areas (see under *Q. glaucoides* below).

In addition to *Q. glaucoides*, several of the species in subsection *Glaucoideae* have prominently glaucous-blue waxy leaves (e.g., *Q. oblongifolia* Torr., *Q. engelmannii* Greene, *Q. splendens*, *Q. subspathulata* Trel., *Q. germana* S. & C., *Q. perpallida* Trel., *Q. depressipes* Trel.). The set of closest relatives of *Q. glaucoides* within subsection *Glaucoideae* probably include one or more of these species. A revised series treatment of species placed in subsection *Glaucoideae* and the relationship of *Q. glaucoides* to other species must await cladistic analyses of the whole group (Nixon, in prog.).

In addition to subsection *Glaucoideae*, fused cotyledons are found in subsection *Virentes* (Loudon) Camus (the southern live oak group). However, the relationship of subsection *Glaucoideae* to the live oaks remains uncertain at this time. Species of *Virentes* differ from *Glaucoideae* in trichome morphology, characters of the cupule, and certain characteristics of germination, and have a distribution that is centered in the southeastern United States and Caribbean. In contrast, no oak species referable to subsection *Glaucoideae* are found east of the Edwards Plateau in the United States.

TAXONOMIC TREATMENT

KEY TO THE SPECIES

Leaves relatively thin, deciduous in winter; petioles (2-)5 – 12 mm long; leaf base rounded or cuneate, decurrent on petiole, occasionally somewhat cordate; fruit usually sessile, the peduncle rarely if ever exceeding 1 cm in length; cupules saucer-shaped or shallowly cup-shaped, enclosing less than one third to one third of the nut, scales usually not strongly tuberculate; nut oblong or barrel-shaped, often flattened at both ends; cotyledons 2, entirely free, easily separable (sometimes adherent in dry material); anthers glabrous 1. *Quercus laceyi*

Leaves coriaceous, persistent through winter, falling in spring or summer of following year; petioles 2 – 5 mm long, thick and expanded basally; leaf base cordate; peduncle of fruit variable in length, from sessile to 4 – 6(-8) cm; cupule thick, hemisphaeric, enclosing one third or more of the nut, scales strongly tuberculate; nut usually globose, rounded distally; cotyledons marginally fused, appearing to be a single mass with a narrow central lumen that widens toward the base; anthers pilose 2. *Quercus glaucoides*

1. ***Quercus laceyi* Small, LACEY OAK (Fig. 1), Bull. Torrey Bot. Club 28: 358. 1901. *Quercus breviloba* Sarg. forma *laceyi* (Small) Trelease, Mem. Natl. Acad. Sci. 20: 102. 1924. *Quercus breviloba* subsp. *laceyi* (Small) A. Camus, Monogr. Genre *Quercus* 2:680. 1936-1938. TYPE: UNITED STATES: TEXAS: Kerr Co.: Lacey's Ranch near Kerrville, 1899-1901, *Howard Lacey s.n.* (NY!).**

Quercus glaucoides of authors.

Trees to 5 – 8 (-10) m; bark light colored, papery or scaly; twigs at first pubescent with erect stellate trichomes, these soon deciduous, at maturity reddish and pruinose to tan and glabrous, 1.5 – 2 mm thick; lenticels scattered, white, usually not prominent; buds ovate to ovate-lanceolate, acute apically, 1.5 – 3 mm long by 1 – 2 mm diam.; bud scales brown with lighter margins, glabrous; stipules rarely persistent around terminal bud; immature leaves with dense vestiture of whitish erect stellate trichomes, these deciduous as the leaves expand; mature leaves thin, deciduous, glabrous, glaucous to yellowish-green, obovate or elliptic in outline, entire to shallowly lobed or occasionally deeply lobed, (2-)4 – 9(-21) cm long by (2-)3 – 6(-11) cm wide; petioles thin, gradually expanding toward base, (3-)5 – 9(-12) mm long; leaf bases cuneate and decurrent on petiole to rounded or rarely somewhat cordate; leaf tip broadly rounded, retuse; leaf margins thin, flat, not cartilaginous; leaf lobes if present oblong, squarish, often retuse; leaf teeth minutely mucronate; primary vein whitish or greenish, raised only on the abaxial surface, not prominently raised above; secondary veins 6 – 9 on each side, each terminating in a tooth or arching near the margins; tertiary veins irregularly percurrent; staminate catkins [pre-anthesis] 15 – 20 mm long; perigon deeply and irregularly cleft, sparsely pubescent externally, margins ciliate; stamens 3 – 4; anthers retuse, sessile, ca. 0.7 mm long, glabrous; pistillate inflorescence to 1(-3) cm long, with 1 – 5 flowers concentrated distally; fruit annual, solitary or

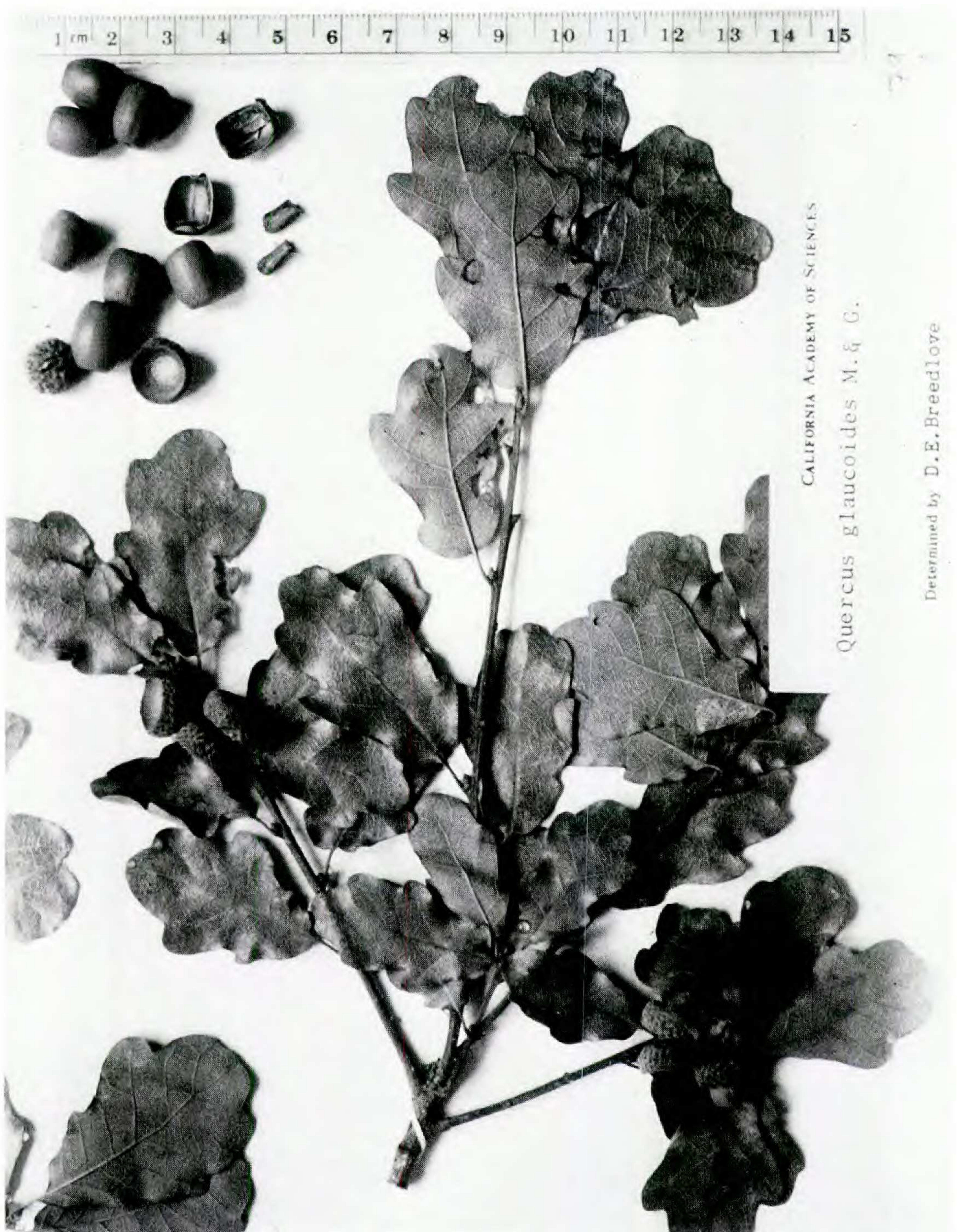


FIG. 1. *Quercus laceyi*. Representative specimen: Coahuila, *Johnston et al.* 12029 (NY).

paired, sessile or on short peduncles to 1(-2) cm in the axils of the leaves; cupule saucer shaped or shallowly cup-shaped, enclosing one third or less of the nut, 10 – 12(-18) mm wide by 4 – 7 mm deep; cupule scales moderately tuberculate, tomentose with detachable hairs; nut oblong or barrel-shaped, often flattened at

both ends, (11-)13 – 15(-20) mm long by 9 – 11(-14) mm in diam.; cotyledons free, equal.

Distribution: Limestone hills, canyons and streamsides, the southern part of the Edwards Plateau of central Texas, southward in the mountainous areas of Coahuila and Nuevo Leon to the vicinity of Galeana and Pablillo, Nuevo Leon, Mexico. On the Edwards Plateau, the species occurs mostly at 350 – 600 meters elevation, while in Coahuila and Nuevo Leon, it typically occurs at much higher elevations, from 1500 – 2200 meters. *Quercus laceyi* may occur in Tamaulipas, but documented records are not known. Sometimes associated with remnant mesic forests which include *Acer grandidentatum* Nutt., *Tilia* spp., *Q. muhlenbergii* Engelm. and various pine and oak species.

Representative specimens: MEXICO: Coahuila: Mun. not recorded: Canyon Hundido, N side of Pico de Centinela, Sierra del Jardín, 1500 – 2250 m, 27 Jul 1973, *Johnston et al.* 11777 (NY); Cañon de la Gavia, S of Rancho de la Gavia, 1250 – 2200 m, 2 – 3 Aug 1973, *Johnston et al.* 12029 (NY); Coahuila: middle part of Sierra San Marcos, 21 May 1983, *Marshall* 83 – 17 (DAV); Sierra la Encantada, north base, 1200 m, 12 Jun 1984, 28° 37'N, 102° 17'W, *Wynd & Mueller* 170 (BH-CHM, MO, NY); Bocatoche, N slope of Sierra del Oso, 2 Sep 1939, *Muller* 3143 (BH-CHM); Mun. Cuatro Ciénegas: Sierra de la Madera: vicinity of “La Cueva” in Corte Blanco fork of Charretera Canyon; scrub-oak zone below the conifer-forests, 5300 – 6500 ft, 11 – 15 Sep 1941, *Johnston* 8933 (BH-CHM); W side of Potrero de la Mula, about 20 km NW of Ocampo, on the escarpment near the mines, 18 Sep 1941, *Johnston* 9207 (BH-CHM); in mid-Canyon de la Hacienda, ca. 35 (air) mi W of Cuatro Ciénegas, 5900 ft, 6 Aug 1973, 27° 04' N, 102° 25' W, *Henrickson & Wendt* 11997 (DAV, TEX); upper Canyon del Pajarito, 6 Sep 1939, *Muller* 3192 (BH-CHM); lower Cañón del Agua, 10 Sep 1939, *Muller* 3267 (BH-CHM); N side, lower part of Canyon de la Hacienda, 1600 m, 11 May 1973, *Johnston et al.* 10977 (NY); upper portion of Cañón de la Hacienda, below first lumber camp, ca. 22 (air) mi WNW of Cuatro Ciénegas, 5000 – 6000 ft, 28 Sep 1973, 27° 04' N, 102° 25' W, *Henrickson* 13627 (DAV); Sierra de la Madera, NW of Cuatro Ciénegas, 1700 m, 24 May 1983, *Marshall* 83 – 19 (DAV); Mun. General Cepeda: Sierra de Parras, near head of Cañón Domingo, 15 Jun 1965, *Muller* 11217 (BH-CHM); Mun. Múzquiz: Hacienda Mariposa, ravine near Puerta Santa Ana, 22 Jun 1936, *F.L. Wynd and C.H. Mueller* 230 (BH-CHM, MO, NY); Sierra del Puerto, Santa Ana, 23 Jun 1936, *Wynd & Mueller* 262 (BH-CHM, MO, NY); Rancho Agua Dulce, E slope of the Sierra de San Miguel, 28 Jun 1936, *Wynd & Mueller* 345, 346 (BH-CHM, NY); Sierra Hermosa de Santa Rosa, 5 mi S of Múzquiz, 2000 – 3000 ft, 8 Jul 1958, *Straw & Forman* 1333 (BH-CHM, DAV); Cañón de las Trancas, Sierra Santa Rosa, 2000 SNM, 25 Oct 1951, *Correa* 2220 (BH-CHM); Sorpresa Spring, 8 Jul 1936, *Marsh, Jr.* 335 (BH-CHM); Sorpresa Spring, 9 Jul 1936, *Marsh, Jr.* 344 (BH-CHM); La Cuesta del Plomo on the Múzquiz-Boquillas Hwy, 1750 – 1775 m, 14 Sep 1972, *Johnston et al.* 9225 (NY); Mun. Saltillo: San Lorenzo Canyon, mountains near Saltillo, 7000 ft, 12 Apr 1906, *Pringle* 10228 (BH-CHM); Mun. Villa Acuña: Serranías del Burro, Rancho El Bonito, Cañón El Bonito, 29° 01' 30" N 102° 07' 30" W, ca. 1650 m, 17 Sep 1977, *Riskind & Valdes* R. 2095 (BH-CHM, TEX); El Bonito, 12 air km W of Rcho. El Bonito HQ, near uppermost stock tank in Cañón El Bonito, 1625 m, 19 Sep 1977, 29° 01' 30" N 102° 07' 30" W, *Riskind et al.* 2200 (BH-CHM); Sierra del Carmen: Canyon de Sentinela [Centinela], Hacienda Piedra Blanca, 6 Jul 1936, *Wynd & Mueller* 541 (BH-CHM, MO, NY), 8 Jul 1936, *Wynd & Mueller* 617 (BH-CHM, MO, NY); canyon E of Mina Popo, ca. 12 (air) mi E of Boquillas, 29 Jul 1973, 29° 13' N, 102° 44' W, *Henrickson* 11560 (DAV, TEX); Sierra del Pino: pine forest in Middle section of the Sierra, 2 – 10 mi N of camp at La Noria, 22 Aug 1940, *Johnston & Muller* 559 (BH-CHM);

W ridge, west of camp at La Noria, 24 Aug 1940, *Johnston & Muller 616* (BH-CHM); Mun. not recorded: 12 km W of Hacienda de la Encantada, E side of the Sierra de los Guajes, Cañón de Milagro, 10 Sep 1941, *Stewart 1507* (BH-CHM); 12 km W of Hacienda de la Encantada, E side of the Sierra de los Guajes, Cañón de Milagro, 10 – 16 Sep 1941, *Stewart 1708* (BH-CHM). **Nuevo Leon:** 33 mi W of Linares, 5 mi W of San Pedro on Hwy 60, 5000 ft, 14 Jun 1972, *Breckon & Breckon 1287* (DAV); ca. 30 mi NE of Dr. Arroyo along Hwy 29 along the first pass, 6000 ft, 9 Sep 1971, 24° 02' N, 99° 58' W, *Henrickson 6617* (DAV); 6.6 mi S of La Escondida on Hwy 68, 5800 ft, 8 Dec 1966, *McIntyre & Gankin 278* (DAV); Linares-Galeana road, half way up the canyon, 3600 ft, 13 Jul 1953, *Manning & Manning 53292* (BH-CHM); 3 mi above Iturbide, on road to Galeana, in oak zone, 2000 m, 18 May 1949, *McVaugh 10561* (BH-CHM); mountains near Monterrey, 15 Jul 1933, *Mueller & Mueller 574* (BH-CHM); Mun. Galeana: Cañón San Francisco, Hacienda Pablillo, 31 Jul 1934, *Mueller & Mueller 1281* (BH-CHM); 23 mi E of Galeana on the Galeana-Linares Hwy, 25 Aug 1938, *Schneider 1119* (BH-CHM); 23 mi E of Galeana on the Galeana-Linares Hwy, 25 Aug 1938, *R.A. Schneider 1120* (BH-CHM); Puerto de Pastores, near Galeana, 5 Jul 1934, *Mueller & Mueller 1001, 1002, 1003* (BH-CHM); Alamar, Hacienda Pablillo, 20 Jul 1934, *Mueller & Mueller 1101* (BH-CHM); Alamar, Hacienda Pablillo, 23 Jul 1934, *Mueller & Mueller 1200* (BH-CHM); Cañón San Francisco, Hacienda Pablillo, 31 Jul 1934, *Mueller & Mueller 1282* (BH-CHM); Cañón San Francisco, Hac. Pablillo, 11 May 1934, *Mueller & Mueller 307* (BH-CHM); Taray, Hacienda Pablillo, 29 May 1934, *Mueller & Mueller 589, 590* (BH-CHM); Mun. Montemorelos: E slope of Sierra de la Cebolla, 21 Aug 1939, *Muller 2941* (BH-CHM); Mun. Villa Santiago: upper slopes of Cañón Guajuco, 14 Aug 1934, *Mueller & Mueller 1353* (BH-CHM).

U.S.A: TEXAS: **Bandera Co.:** Lost Maples State Park, N of Vanderpool, 9 Jun 1984, *L.E. Brown 7504* (BRIT/SMU); 9 mi W of Tarpley, Utopía to Bandera, just over fence N side of Hwy, 1600 ft, 13 Aug 1953, *Harris 289* (BH-CHM); Vanderpool, 11 Apr 1917, *Palmer 11535* (MO); Medina Lake, 14 Jun 1917, *Palmer 12264* (MO); Upper Seco Creek, 18 Jun 1916, *Palmer 10233* (MO). **Brewster Co.:** E Slope of Solitario Mt., canyon headers, 3800 ft, 20 Aug 1974, *Warnock 23860* (BH-CHM). **Edwards Co.:** 14.5 mi SE of Rocksprings, 9 Aug 1943, *V.L. Cory 42935* (BRIT/SMU); 10 mi SE of Rock Springs, 3 Apr 194-, *Muller 5155* (BH-CHM); 23 mi N of Brackettville on road to Rock Springs, 15 Jun 1945, *Muller 8086* (BH-CHM); 23 mi N of Brackettville on road to Rock Springs, 15 Jun 1945, *Muller 8087* (BH-CHM); Barksdale, 11 Oct 1916, *Palmer 10996* (MO); Nueces Rd., 11 Sep 1929, *Tharp s.n.* (MO). **Kerr Co.:** Rocky bluffs of Upper Cebelo River, near Boerne, 30 Sep 1917, *Palmer 12903* (MO, NY); Upper Cebelo Creek, 29 Sep 1916, *Palmer 10863* (MO). **Kerr Co.:** ca. 14 mi W of Kerrville, Turtle creek, 29 Sep 1946, *V.L. Cory 52407* (BRIT/SMU, NY); Kerrville, rocky bluffs of Guadalupe River, 7 May 1928, *Palmer 33796* (MO, NY, TEX); 2 mi SE of Mountain Home, 16 mi NW of Kerrville, near the E bank of the Guadalupe River, 5 Jun 1942, *Muller 5022* (BH-CHM); W bank of Guadalupe River at Ingram, 7 mi NW of Kerrville, 5 Jun 1942, *Muller 5021* (BH-CHM); Kerrville, 2 Oct 1916, *Palmer 10884* (MO); Lacey's Ranch, 28 Mar 1916, *Palmer 9284*; 3 Oct 1916, *Palmer 10889* (MO). **Kimble Co.:** South Llano River, Telegraph, 9 Oct 1916, *Palmer 10952* (MO). **Medina Co.:** Medina Dam, Oct 1938, *Parks s.n.* (DAV). **Menard Co.:** Menard, 12 May 1917, *Palmer 11895* (MO). **Real Co.:** ca 11 mi N of Hackberry, 10 Jul 1943, *Cory 42619* (NY); 17 mi W of Camp Wood, 2000 ft, 19 Jun 1953, *V.M. Harris 24* (BH-CHM); 13 mi E of Camp Wood, on Hwy between Camp Wood and Leakey, 2000 ft, 21 Jul 1953, *Harris 172* (BH-CHM); 3 mi SE Camp Wood, Z. B. Gray Ranch, 1500 ft, 24 Jun 1953, *Harris 55* (BH-CHM); Barksdale, 7 May 1918, *Palmer 13516* (MO); Leakey, 10 Jun 1916, *Palmer 10152* (MO). **Terrell Co.:** 16 mi S of Sheffield, in Little Horse Head Canyon, Blackstone Ranch, 27 Jun 1949, *Webster 429* (BH-CHM); 16 mi S of Sheffield, in Little Horse Head Canyon, Blackstone Ranch, 27 Jun 1949, *Webster 431* (BH-CHM). **Uvalde Co.:** 6 mi S Montell, Y.A. Coleman Ranch, 1250 ft, 23 Jul 1953, *Harris 177* (BH-CHM); 6 mi S of Montell, Y.A. Colemannders, just over fence N side of

Hwy, 1250 ft, 24 Jun 1953, *Harris 43* (BH-CHM); 8 mi N of Uvalde, the Dry Frio River, 27 Jun 1942, *Muller 5045* (BH-CHM); valley of the Dry Frio River, 8 mi N of Uvalde, 27 Jun 1942, *Muller 5054A* (BH-CHM); Uvalde, 14 Oct 1916, *Palmer 11042* (MO); Concan, 14 Jun 1916, *Palmer 10187* (MO); Without county data: W Fork of Nueces River, Oct 1883, *Havard 4* (BRIT/SMU, MO).

2. *Quercus glaucoides* Mart. & Gal. (Fig. 2), Bull. Acad. Brux. 10(1):209. 1843. TYPE: MEXICO. Oaxaca: Mixteca Alta, 2600 m, Jun 1840, *Galeotti 103* [*Schiede 103*] (HOLOTYPE: BR!; ISOTYPES: C!, G-DC!, K!).

Quercus cordata Mart. & Gal., Bull. Acad. Brux. 10(1):211. 1843. TYPE: MÉXICO: OAXACA: Mixteca Alta, *Galeotti 111* (Type specimen lost, fide Trelease, 1924:53; subsequent search has been unsuccessful). *Q. cordata* has long been considered a synonym of *Q. glaucoides*. The protologue of *Q. cordata* is consistent in locality and description with the holotype of *Q. glaucoides*, which we select as neotype for this name. NEOTYPE here chosen: MÉXICO. OAXACA: Mixteca Alta, 2600 m, Jun 1840, *Galeotti 103* [*Schiede 103*] (HOLOTYPE: BR!; ISOTYPES: C!, G-DC!, K!).

Quercus glaucophylla v. Seem., Bot. Jahrb. 29:95. 1900. TYPE: MÉXICO. OAXACA: Sierra de San Felipe, 27 Aug 1895, *Pringle 4843* (HOLOTYPE: BR!; ISOTYPE: BM!, G!, K!, BH-CHM[ex G]!).

Quercus baldoquinae Trelease, Mem. Natl. Acad. Sci. 20:53. pl. 43. 1924. TYPE: MÉXICO. MICHOACAN: Cerro Baldoquin, *Endlich 1354* (HOLOTYPE: B, presumed destroyed). Trelease cited only the single specimen, and Endlich material apparently was not distributed to other herbaria. LECTOTYPE here chosen: Trelease's original plate 43.

Quercus cancellata Trelease, Mem. Natl. Acad. Sci. 20:55. pl. 49a, 49b. 1924. TYPE: MÉXICO. PUEBLA: Sierra de Mixteca, 24 Aug 1908, *Schenck 236* (HOLOTYPE: B, presumed destroyed). The single paratype cited, *Schenck 92*, the basis of plate 49b, was also at B and was similarly destroyed. Duplicates of *Schenck* collections are not known. LECTOTYPE here chosen: Trelease's original plate 49a.

Quercus conjungens Trelease, Mem. Natl. Acad. Sci. 20:55. pl. 48a, 48b. 1924. TYPE: MÉXICO. GUANAJUATO: Acambaro, at 1900 m, 6 Oct 1904, *Pringle 8841* (HOLOTYPE: B, presumed destroyed; LECTOTYPE here chosen: G-BOISS!; ISOTYPES: BH-CHM![ex G], M!, K!, TEX!).

Quercus mixtecana Trelease, Mem. Natl. Acad. Sci. 20:54. pl. 46. 1924. TYPE: MÉXICO. PUEBLA: Sierra de Mixteca, San Luis, 16 Aug 1908, *Schenck 235* (HOLOTYPE: B, presumed destroyed). As with *Q. cancellata*, no extant *Schenck* collections are known, and no other specimens were cited. LECTOTYPE here chosen: Trelease's original plate 46.

Trees to 10 m, usually less than 5 m tall, bark scaly and gray or sometimes darker and deeply furrowed; twigs 1–2 mm thick, yellowish-tomentulose when very young, soon glabrous, gray to reddish brown, with numerous small round whitish corky lenticels; buds 2–4 mm long, ovoid or rounded, dark brown; bud scales glabrous, with waxy or ciliate margins; stipules linear-subulate, 6–9 mm long, pilose, deciduous or occasionally persistent around terminal buds; immature leaves reddish, clothed with yellowish curly fasciculate trichomes that are soon deciduous as the leaves expand; mature leaves coriaceous, thick, glaucous green, persisting a full year, oblanceolate to oblong, elliptic or obovate, (4-)6–12(-15) cm long, 2.5–5(-8) cm wide, 2–2.5 times as long as wide; petioles 2–6 mm long, 1–2.5 mm thick at the abruptly swollen base, reddish with a waxy pruinose bloom; leaf base cordate or occasionally rounded; leaf tip rounded,



FIG. 2. *Quercus glaucooides*. Representative specimen: Guerrero, Hinton *et al.* 9051 (NY).

sometimes broadly retuse; leaf margins cartilaginous, not revolute, usually undulate, entire or with 1 – 7 broad, often antrorse teeth on each side; leaf teeth each with a darkened callous or “glandular” thickening terminating the secondary vein; primary vein straight, prominent and yellowish, raised on adaxial and abaxial surface of the blade at least toward base; secondary veins 6 – 12 on each side, each terminating in tooth or arching near the margin and eventually

anastomosing with next distal secondary vein; tertiary veins percurrent, arched and sometimes branched; staminate catkins 2 – 3 cm long, densely hairy; anthers pilose, 1 – 1.6 mm long. Pistillate inflorescence to 1 – 8 (-20) cm long, with 2 – 3 (-8) flowers, these often scattered along rachis; fruit annual, solitary or 2 – 3, subsessile in the leaf axil or more often on a peduncle 1 – 6 cm long; cupule turbinate or hemispheric, 12 – 18 mm wide, the scales brownish or yellowish tomentulose, often prominently tuberculate except near the rim of the cupule; nut ovoid or oblong-barrel-shaped, 12 – 18 mm long, one third to one half included; cotyledons marginally fused, the free central lumen wider toward the base of the seed.

Distribution: A widespread and common species, often on limestone, at 1000 – 3000 meters elevation, in dry tropical deciduous forest, dry oak woodland, dry pine-oak forest and margins of thorn scrub in Guerrero, Hidalgo, Jalisco, Mexico, Michoacan, Nayarit, Oaxaca, Puebla, San Luis Potosi, Sinaloa, and Zacatecas. Not known to overlap in range with *Q. laceyi*.

Quercus glaucoides apparently hybridizes in nature with few other species of oak. Morphologically intermediate specimens between *Q. glaucoides* and *Q. splendens* Nee, as well as *Q. peduncularis* Nee, have been noted, but are not common.

Representative specimens: MEXICO. Estado unknown: *Liebmann 105=3489* (BH-CHM). GUERRERO. District Of Mina: Los Barrales, 4 Jul 1939, *Hinton et al. 14393* (NY); Placeres, 6 Jul 1936, *Hinton et al. 9051* (NY); Parotas, 1260 m, 5 Aug 1936, *Hinton et al. 9198* (NY); Cerro de la Mesa, Coyuca de la C. Gro., Nov 1951, *García 2179* (BH-CHM); Chilpancingo, Jalapa, km 13.5 en carretera a Chichihualco, 1560 m, 30 May 1968, *Kruse 1815, 1816* (BH-CHM); Mazatlán, falda este del cerro El Alquitrán, 1380 m, 16 Jun 1968, *Kruse 1849* (BH-CHM); Chilpancingo, Jalapa, km 13.5 en carretera a Chichihualco, 18 Jul 1968, *Kruse 1888, 1889* (BH-CHM); Chilpancingo, Jalapa, km 13.5 en carretera a Chichihualco, 1480 m, 6 Oct 1968, *Kruse 2012* (BH-CHM); 3 km NE of Huajojutla, 13 km NE of Taxco, 12 Oct 1951, *Muller 9157, 9158, 9159* (BH-CHM); Cerro Tres Piedras, Cutramalia, 8 Oct 1951, *Narciso Santamaría 2180* (BH-CHM); Cerro de la Mesa, Coyuca de la C. Gro., Nov 1951, *Tabares 2183* (BH-CHM). HIDALGO: Mun. Pachuca: SE of Epazoyucan, 2500 – 2700 m, 14 Jun 1947, *Moore 3058* (BH, BH-CHM); JALISCO: 20 – 25 mi NNW of Guadalajara, between Milpillas and Escalón, near summits of hills falling off into barranca of Río Grande, 12 Apr 1951, *McVaugh 11970* (BH-CHM); Cerro de García, Tuxcueca, 8 mts y 1,570 mts, 2 Aug 1951, *Jose León Navarri 2060* (BH-CHM); 1 km al E de Mata de Bule, cerca de Los Corales, 25 Oct 1963, *Rzedowski s.n.* (BH-CHM); Mun. Tecalitlan: Barranca de San Juan de Dios, cerca de Los Corales, 1300 m, 23 Oct 1963, *Rzedowski 17373* (BH-CHM); 1 km al E de Mata de Bule, cerca de Los Corales, 1200 m, 25 Oct 1963, *Rzedowski 17484* (BH-CHM). ESTADO DE MEXICO. District of Temascaltepec: Tejupilco, 7 Sep 1934, *Hinton 6561* (NY); Mun. Valle de Bravo: Pine-oak forest between Tiloxtoc and San Bartolo, NW of Valle de Bravo, 26 Sep 1951, *Muller 9098* (BH-CHM, NY); 1 km S of Chalma, 23 Oct 1951, *Muller 9219* (BH-CHM); Cerro de Moctezuma, Los Remedios, Naucalpán, 2 Nov 1951, *Rodríguez 2145, 2251, 2252* (BH-CHM). MICHOACÁN. Zitacuaro-Coyota, 25 Aug 1938, *Hinton et al. 13099* (NY); slopes of Cerro Potrerillos, ca. 5 mi N of Cotija and 22 mi S of Jiquilpán, 5 – 9 Oct 1961, *King & Soderstrom 4655* (NY); W slopes of Cerro de Carboneras, ca. 22 km S of Utruapán, 3300 – 3700 ft, 16 – 22 Oct 1961, *King & Soderstrom 4914* (NY); 12 km W of Zamora, at lower limit of oaks, 19 Sep 1951, *Muller 9061* (BH-CHM); 2 km al SE de Palo Alto, 22 Mar 1963, *Rzedowski 16333* (BH-CHM); Mun. Cojumatlán: 2 km al SE

de Palo Alto, 1600 m, 22 Mar 1963, *Rzedowski s.n.* (BH-CHM). MORELOS. Noroeste de Cuernavaca km 85 carretera Cuernavaca-Tepoztlanco, 1730 m, 5 May 1965, *Palácios 12* (BH-CHM); 8 km al Noroeste de Cuernavaca km 8 carretera Cuernavaca-Tepoztlanco, 1750 m, 5 May 1965, *Palácios 2* (BH-CHM). OAXACA. Canyon of the Río Zavaleta near San Pablo Quatro Venados, 15 – 18 km WSW of Oaxaca, 20 – 25 Jan 1937, *Camp 2549* (NY); Sierra de San Felipe, 6000 ft, 27 Aug 1894, C.G. *Pringle 4843* (NY); 4 km SW of Magdalena Jicotlan, district of Coixtlahuaca, 2300 m, 17 May 1968, *Rzedowski 25715* (NY); Near San Juan del Estado, Oaxaca Valley, 7 Nov 1894, *Smith 779* (NY); Río Flor, S Pedro Jilotepec, 1000 m, 29 Oct 1952, *MacDougall 2424* (BH-CHM); Río Flor, S Pedro Jilotepec, 28 Oct 1952, *MacDougall 2426* (BH-CHM); Tenango, 3000 m, 30 Oct 1952, *MacDougall 2430* (BH-CHM); Montaña en el camino a Chilapa de Matamoros, 2000 mts, 1 Apr 1953, *Matuda 28421* (BH-CHM); 10 km NW of Tamazulapán, in the Mixteca Alta, Cerro Encinal above Santa María de Tutla, 23 Nov 1951, *Muller 9395* (BH-CHM); 6 km NW of Huitzo, 42 km NW of Oaxaca, in the Mixteca Alta., 23 Nov 1951, *Muller 9412* (BH-CHM); 4 km above and SE of Matatlan, 25 Nov 1951, *Muller 9414* (BH-CHM); 7 km E of El Camarón, 25 Nov 1951, *Muller 9416, 9417* (BH-CHM); 7 km SE of Portillo de Nejapa, 18 km SE of Camarón, 2 Dec 1951, *Muller 9457* (BH-CHM); foothills of Sierra de San Felipe, 3 km NE of San Juan del Estado, 25 km NW of Oaxaca, 3 Dec 1951, *Muller 9461* (BH-CHM). PUEBLA. Cerro de Gavilán, 7000 – 8000 ft, Aug 1909, *Purpus 4090* (NY); Zapotitlán Valley, between Calipa and Acatepec, 1200 to 2000 m, 20 Jul 1961, *Smith et al. 3994* (NY); 3 km NNW of Tepehene, 15 km SSE of Izúcar de Matamoros, 22 Nov 1951, *Muller 9385* (BH-CHM); 10 km SSE of Las Peñas, 16 km NNW of Acatlán, 22 Nov 1951, *Muller 9386* (BH-CHM); 4 km SE of Chila, 4 km NW of Oaxaca state line, 22 Nov 1951, *Muller 9389* (BH-CHM); Valle de Bravo: 3 km N of Santo Tomás de los Plátanos, edge of the Tierra Caliente, 1400 m, 25 Sep 1951, *Muller 9083* (BH-CHM).

ACKNOWLEDGMENTS

We thank Enrique Estrada for the Spanish translation of the abstract. We also thank the curators of B, BM, BR, BRIT/SMU, C, DAV, G-DC, K, M, MO, NY, and TEX for use of specimens and types examined in this study. In addition to the above curators, John Tucker was extremely helpful during a visit to DAV; likewise Nancy Morin at MO. Other herbaria are not cited in part due to inavailability of material on loan to another worker during the course of this study. Richard Jensen and an anonymous reviewer provided thoughtful and helpful comments on the manuscript, but the authors are solely responsible for any errors or omissions.

REFERENCES

- BELLO G., M.A. and J. LABAT. 1987. Los Encinos (*Quercus*) del Estado de Michoacán, Mexico. Centre D'Etudes Mexicaines et Centramericaines. Mexico.
- DORR, L.J. and K.C. NIXON. 1985. Typification of the oak (*Quercus*) taxa described by S.B. Buckley (1809 – 1884). *Taxon* 34:211 – 228.
- McVAUGH, R. 1974. Flora Novo-Galiciana. Fagaceae. *Contr. Univ. Michigan Herb.* 12:3 – 93.
- MULLER, C.H. 1951. The oaks of Texas. *Contr. Texas Res. Found.* 1:21 – 323.
- _____. 1970. *Quercus*. In: D.S. Correll and M.C. Johnston, *Manual of the vascular plants of Texas*. pp. 467 – 492. Texas Research Found., Renner, Texas.
- NIXON, K.C. 1985. Cotyledon characters of Mexican white oaks: distribution and phylogenetic significance of fused cotyledons. Abstracts of A.I.B.S. meetings, Indiana University.

SMALL, J.K. 1901. Shrubs and trees of the southern United States.-IV. Bull. Torrey Bot. Club 28:356 – 361.

TRELEASE, W. 1924. The American oaks. Mem. Natl. Acad. Sci. 20:1 – 255.